Distribution patterns of ocellated eagle rays, *Aetobatus ocellatus,* along two sites in Moorea Island, French Polynesia

by

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Abstract. – Elasmobranchs are critical to tourism industries worldwide. In French Polynesia, where ecotourism is the second most important industry, little is known about the spatiotemporal distribution of eagle rays. This study represents the first investigation into habitat use and behaviour of ocellated eagle rays (*Aetobatus ocellatus*) in French Polynesia focused on two sites with different levels of anthropogenic noise. Environmental variables and biological data were recorded over a one-year period to explore the distribution patterns of 113 eagle rays identified at these sites. Results revealed distinct patterns in habitat use between the two sites, with the eagle ray population structured according to ontogenetic stage. Young rays preferred the site with lower levels of noise pollution, where they foraged at the end of the day. Adult eagle rays gathered in the mornings at the louder site, where the only noticeable activity was group swimming. Overall, our results could help conservation initiatives to manage this important species in French Polynesia, and potentially other coral reef areas, especially in the context of rising human impacts on the environment.

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Résumé. – Modèles de répartition de la raie aigle léopard, *Aetobatus ocellatus*, dans le lagon de Moorea, Polynésie française.

Les élasmobranches sont des espèces clés de l'écosystème corallien et sont aussi indispensables à l'industrie de l'écotourisme. En Polynésie française, où l'écotourisme est le second pilier économique, peu d'information est disponible sur la répartition spatio-temporelle des raies aigle. Cette étude présente la première investigation de l'utilisation de l'habitat et du comportement de la raie aigle léopard (*Aetobatus ocellatus*) sur deux sites (Mareto vs. ClubMed) de la côte Nord de Moorea. Ces sites diffèrent entre autre par le bruit anthropique, le site ClubMed étant beaucoup plus bruyant que le site Mareto du fait de l'activité nautique. Pendant une année, différentes variables environnementales et biologiques ont été enregistrées afin de comprendre le modèle de répartition des raies aigles (113 individus observés). Les résultats montrent une utilisation différente des deux sites, avec des préférences significatives selon le stade ontogénique. Les juvéniles ont une préférence pour le site de Mareto où ils viennent se nourrir à la fin du jour. Les adultes se rassemblent le matin au site du ClubMed, où l'activité principale est la nage en groupe. Au final, notre étude fournit de premières observations essentielles sur la connaissance de la distribution spatio-temporelle des raies aigles à Moorea sur deux sites soumis à des activités anthropiques différentes.

Key words
Animal behaviour
Ontogenetic partitioning
Photo-identification
Anthropogenic activities
Rays

Animals choose a habitat that enhances fitness or that is best for their particular ontogenetic stage (Papastamatiou *et al*. 2009; Grubbs, 2010; Speed *et al*., 2010; Delaney and Warner, 2016), or sex (Delaney and Warner, 2016), with low predation risk and high prey availability (Heupel and Hueter, 2002; Glaudas and Rodríguez-Robles, 2011). In elasmobranches for example, white shark males and females have different foraging strategies, which lead them to different habitats best suited for them (Bruce and Bradford, 2015), and it is well documented that whale sharks and manta rays migrate according to plankton productivity (Wilson *et al*., 2001; Anderson *et al*., 2011). However, little is known about the habitat selection of the ocellated eagle ray *Aetobatus ocellatus* (Kuhl, 1823) in French Polynesian lagoons. The ocellated eagle ray is a benthopelagic, large body-sized ray, occurring in the tropical area of the Indo-West Pacific

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(Schluessel *et al.*, 2010; Berthe *et al.*, 2016a). The ocellated eagle ray occurs in the Society and Tuamotu archipelagos of French Polynesia (Berthe *et al.*, 2016b) where they can be observed in large schools as well as alone (Berthe *et al.*, 2016b; Berthe and Lecchini, 2016). However, some important questions have remained unanswered: 1) do ocellated eagle rays in Moorea have a seasonal or tidal cycle; 2) is the Moorea Island lagoon used for any important ecological processes (*e.g.* nurseries area); 3) are the groups of rays segregated by gender or ontogenetic stage? Better understanding of this species' life history is needed as low reproductive rates (1-4 pups annually) combined with intense and unregulated inshore exploitation have led to the ocellated eagle ray being listed as "near threatened" globally and "vulnerable" in Southeast Asia (Kyne *et al.,* 2016). In French Polynesian waters, fishing for any of the 25 different species of sharks and rays inhabiting French Polynesian waters has been prohibited since 2011 (Siu *et al.*, 2017). Elasmobranches are important to the Polynesian economy in the form of ecotourism activities, which brings in around USD$140 million annually for manta ray watching alone (O'Malley *et al.*, 2013), and in the cultural history of Polynesia (Clua and Guiart, 2015). Although *A. ocellatus* does not directly suffer from bycatch or fishing pressure in this region, it does face other anthropogenic stressors in their inshore habitats, such as habitat loss or habitat degradation because of increased noise, pollution or light (Berthe and Lecchini, 2016). Here, we launched the first study on the ocellated eagle ray in French Polynesia to explore the spatial and temporal patterns in the presence of adult and juvenile eagle rays at sites differing in levels of anthropogenic noise and habitat quality. Our results could help conservation initiatives to manage this important species in French Polynesia, especially in the context of rising human impacts on the environment.

MATERIALS AND METHODS

Study site

Ocellated eagle rays were studied along the north coast of Moorea, French Polynesia. A preliminary investigation around Moorea identified sites where eagle rays are abundant (Berthe, 2017). Most of them were located in the deeper passes of the island, where there is strong current, poor visibility and high boat traffic, making it impossible to conduct regular surveys, however two sites located within the lagoon were also identified (Fig. 1). The Mareto site, located on the east side of Opunohu Bay, is 350 m long and 180 m wide, with depths ranging from 2 to 7 m. The ClubMed site, located on the west side of Opunohu Bay, between the main island and two small inlets, is 400 m long and 180 m wide, also with depths ranging from 2 to 7 m. The two locations have the same topography, which consists of a sandy area, a channel, and a fringing reef. However, human influence on the two sites differs. Mareto is a public beach and a mooring area, with boats travelling at low speed; while ClubMed is a channel where boat traffic is heavy (*e.g.* glass bottom boats, jet-skis, dive boats, transfer boat, etc.) year-round.

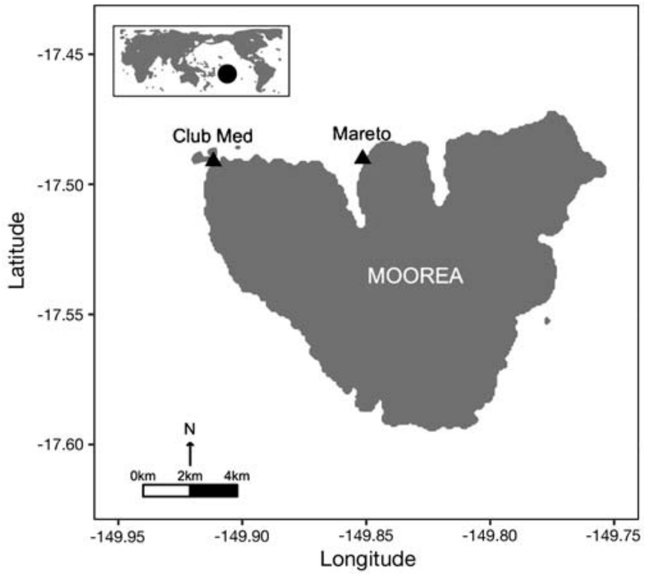

Figure 1. – Map highlighting the two study sites on Moorea Island, French Polynesia: Mareto and ClubMed.

Photo-identification

Photo-identification has been used for many marine species, using marks such as mating scars or wounds, body shape or even dorsal pattern (*e.g.* Anderson and Goldman, 1996; Brooks *et al.*, 2010). We took > 1000 photos of ocellated eagle rays between September 2014 and October 2015 using a Canon G16 in an underwater housing (Fantasea, Blaine, WA, USA). Only photos where dorsal pattern was sharp were used for comparison. Photos were first manually analyzed using the entire dorsal pattern of the animal. They were then analyzed using I3S Pattern software (v4.02, van Tienhoven *et al.*, 2007) using the right fin pattern.

Underwater visual surveys and environmental data

Visual surveys (n = 89) were conducted to record ocellated eagle rays in the two study sites in the morning or afternoon from September 2014 to October 2015. To do this, a single observer would snorkel at the site with a mechanical flowmeter (General Oceanics, mechanical flowmeter model 2030 series) and a digital video camera (Canon G16). The observer recorded environmental parameters and counted boats and jet-skis at the site. Rays were counted and sex and ontogenetic stage characterized: male = individual larger than 70 cm disk width with apparent claspers; female = individual larger than 70 cm disk width without claspers; and juvenile = individual smaller than 70 cm disk width without apparent claspers (Berthe and Lecchini, 2016). Moreover, the dominant behaviour of the eagle rays was also recorded: swimming, foraging, pre-mating, cruising, jumping, chafing, escaping, interacting with conspecifics or heterospecifics, and interacting with the observer. A multiple correspondence analysis (MCA) coupled with general linear models (GLM) was conducted to identify the relationships between sex and ontogenetic stage of rays, site, season, and time of the day.

At each survey on one site, the date (day, month, and year) and the time (morning: from midnight to noon, afternoon: from noon to midnight) of the day were recorded (surveys were regularly done throughout the study to remove temporal bias). The wind speed (ordinal variable), wind direction (nominal variable), wave direction (nominal variable), wave height (ordinal variable), and tidal data (ordinal variable) were obtained via online forecast (http://fr.surf-forecast.com/). Prevailing current speed (ordinal variable) was recorded using a mechanical flowmeter (General Oceanics mechanical flowmeter model 2030 series). According to their frequency distribution, ordinal variable values were split into groups: low (0-15 km/h), medium (16-30 km/h) and high (31-45 km/h) for wind speeds; no (no current), light (0-10 cm/s), medium (10-20 cm/s), and strong (more than 20 cm/s) for current strength. In order to link the spatial (Mareto vs. ClubMed) and temporal (September 2014 to October 2016) distribution of eagle rays to the six environmental parameters, a multiple factor analysis (MFA) was performed (Escoffier and Pages, 1994). The spatiotemporal distribution of males and females and between adults and juveniles and the six environmental variables were used as the first and second sets of variables for this analysis. The different clusters identified according to environmental variables provided resultant components that were analyzed by MANOVA (conducted on environmental variables and the abundance of rays between the two sites), and ANOVA with a *post hoc* Tukey's test for multiple comparisons (conducted on the interaction: abundance of each ontogenetic stages vs. sites).

Benthic analyses

Benthic sampling was conducted once at each site (October 2015) to determine the potential prey items on which the ocellated eagle rays would be foraging. An air pump and a 2 mm mesh bag were used to excavate the upper 15 cm^2 of sand from five random locations at each study site. Each sample was sieved through a 2 mm mesh, and the macrobenthic fauna was then identified to the genus level (Carpenter and Niem, 1998), counted, and weighed. Abundance (macroinvertebrate) and biomass were compared, between the two sites using Wilcoxon-Mann-Whitney rank sum tests. All statistical analyses were performed in R 2.15.0.

RESULTS

Using photo-identification, 113 unique individual eagle rays were identified during the 89 surveys performed: 40 males, 43 females, and 30 juveniles, including 67 individuals at ClubMed and 47 and Mareto (Tab. I). A single individual was observed at both sites (a juvenile at the Mareto site in October 2014, which had matured to the adult stage at the ClubMed site in September 2015). This instance was the only example of inter-site movement observed during the survey. Of all of the individuals identified at ClubMed, 99% were adult, while 64% of the individuals recorded at Mareto were juveniles.

Spatiotemporal distribution

During the 89 surveys performed for this study, 521 rays were recorded. Of the 113 individual rays identified, 40% were observed only once, while 21% were observed at least on 6 different occasions. No significant difference was observed in the number of surveys conducted during the dry (June to September) vs. wet (October to May) or the morning vs. afternoon periods at each site (Pearson's chi-squared test with Yates' continuity correction, p-value > 0.20). A multiple correspondence analysis (MCA) coupled with GLM highlighted the relationships between ontogenetic stages of rays, sites, season, and time of the day (Fig. 2). The MCA separated the ontogenetic stage of rays and the sites along the axis 1 (35% of the total variance). Axis 2 separated the ray sex, the season and the time of day (20% of the variance). The GLM showed that when one factor was analysed (ontogenetic stage, site, season, or time of day), all results were significant (*e.g.* factor "site": z value = 10.81, p-value < 0.001). When the two-way interaction was analysed, all results were significant (*e.g.* for site and time of the day: z value = –7.27, p-value < 0.001), except for the interaction between "site" and "season". When the interaction between three or all factors were analysed, results were not significant. Overall, the GLM and MCA analyses showed that, irrespective of season, there were significantly more adult males and females at the ClubMed site and more juveniles at the Mareto site, and there were significantly more rays in the morning at the ClubMed site and more rays in the afternoon at the Mareto site (Fig. 2).

Table I. – Counts of eagle rays (*Aetobatus ocellatus*) that were observed; totals for adults are separated by sex. Juvenile column represents individuals under 70c m width, when sex was not possible to determine. Numbers in parentheses indicated identified individuals.

Location	Males	Females	Juveniles	Total
ClubMed	244 (31)	145 (35)	1 (1)	390 (67)
Mareto	14 (9)	10 (8)	107 (30)	131 (47)
Total	258 (40)	155 (43)	108 (30)	521 (113)

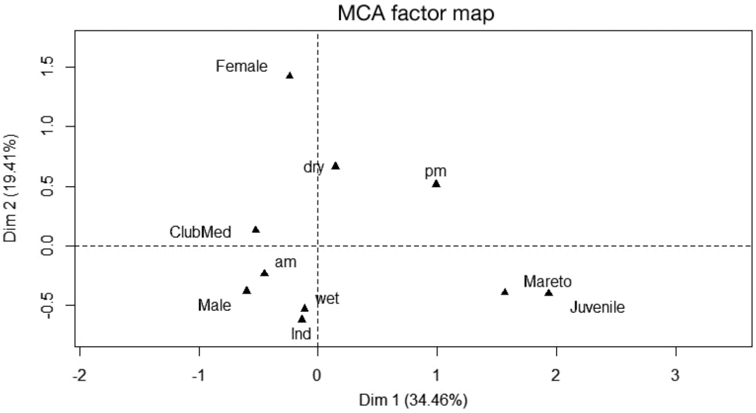

Figure 2. – Multiple Correspondence Analysis factor map (2 first components, 34.5% and 19.4%, respectively) representing the relationship between the study sites (ClubMed/Mareto), ontogenetic stage of the eagle rays (male/female/juvenile), seasons (wet/dry), and the time of the day (am/pm).

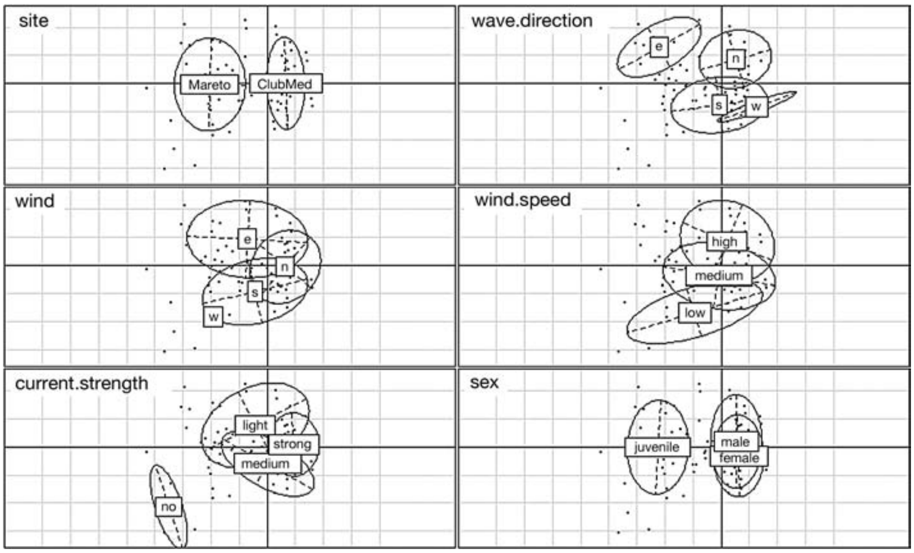

Figure 3. – Multiple Factor Analysis scatter plots (2 first components, 18% and 13%, respectively) representing the relationship between sex (male/ female/ juvenile), the site (ClubMed/Mareto) and the environmental factors: wave and wind direction (east/north/south/ west), wind speed (high/medium/low) and current strength (no/light/medium/ strong).

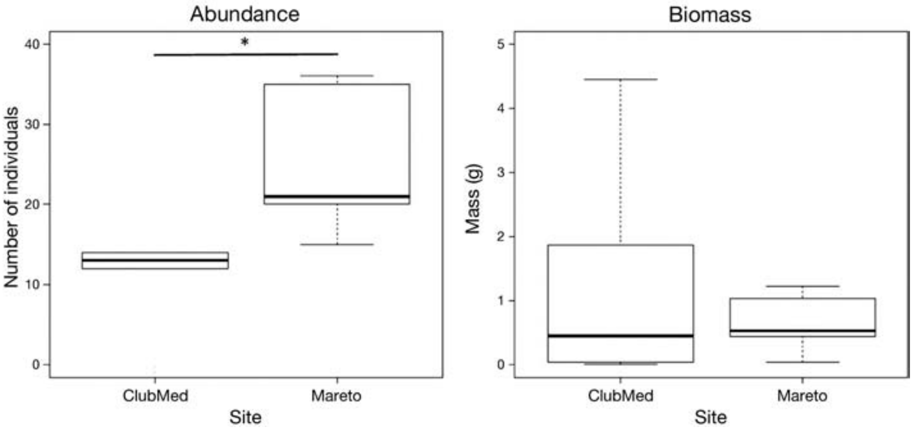

Figure 4. – Abundance (number of macroinvertebrate individuals) and biomass (grams) for the two study sites. The boxes represent the first and third quartiles, black lines are the medians (second quartiles), and whiskers correspond to the range (min-max) of the distributions. An asterisk indicates statistically significant differences.

Influence of environmental factors on the spatiotemporal distribution

Firstly, results from the MANOVA showed that wind speed, wind direction, wave direction, and current speed significantly influenced the abundance of rays between the two sites (p-values of all environmental parameters < 0.05). Secondly, results from the MFA revealed a separation between the juvenile rays occupying the Mareto site and the adult male and female rays occupying the ClubMed site with three of the four environmental variables along the X axis (explaining 40% of variance; Fig. 3). Thus, the juvenile rays were more abundant at the Mareto site when there was no

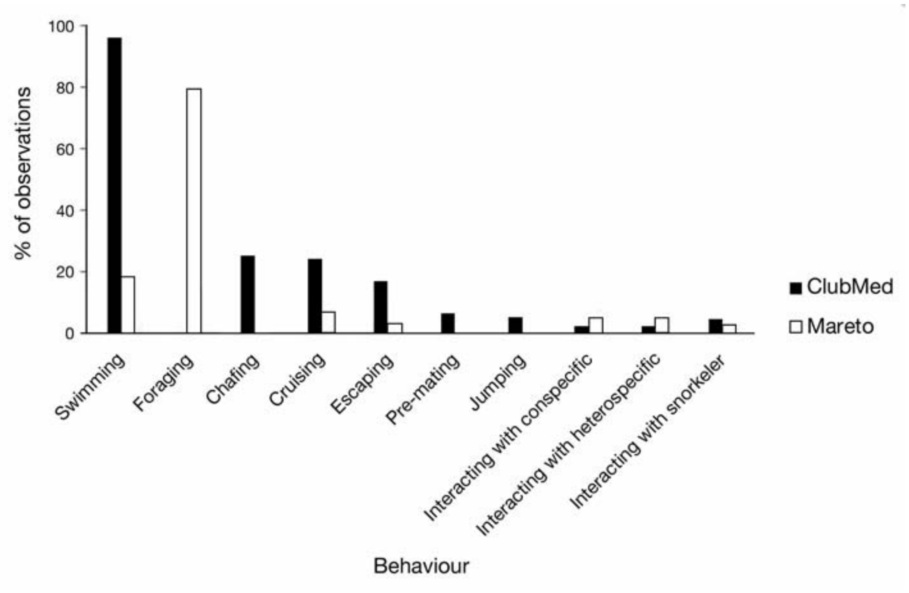

Figure 5. – Percentage of observations for the ten different behaviours according to the study site: swimming, foraging, chafing, cruising, escape, pre-mating, jumping, conspecific interaction, heterospecific interaction, come-close. See Table II for details on each behaviour.

Table II. – Description of the different kind of behaviours observed during the study.

Behaviour	Description of the behaviour	Number of ind. involved
Swimming	Individual or group of individuals swimming against the current, like suspended in the water column, doing nothing special	1 or more
Cruising	Moving individual or sub-group of individuals who swim by, swim to or out of the group	1 or more
Foraging	Searching into the substrate to eat	1
Chafing	Chafing against the substrate or using cleaning station in order to remove exoparasites	1 or more
Pre-mating	Male gripping a female on her back	2
Come close	Swim to the observer	1
Jumping	Jump out of the water	1
Conspecific interaction	Other interaction than previous (e.g. two males fighting)	2 or more
Heterospecific interaction	Interaction with other species	1 or more
Escape	Swimming at least 50 m away from the foraging or swimming site when a boat passed by	1 or more

current and/or an east or west wind (ANOVA and Tukey's test, all p-values < 0.001). In contrast, the female adult rays were more abundant at the ClubMed site when the wind was coming from the north at a medium or high speed and when there was a westward or northward wave direction (ANOVA and Tukey's test, all p-values < 0.05). The abundance of male adult rays at the ClubMed site did not correlate with any of the environmental variables measured. Lastly, the Yaxis of the MCA did not discriminate the spatial distribution of eagle rays according to the environmental variables.

Benthic analyses

The comparison of the two study sites according to prey availability showed a significantly higher abundance of prey at Mareto site than at the ClubMed site (Wilcoxon-Mann-Whitney, W = 3, p-value < 0.05), with a density of 170 ind/m^2 and 91 ind/m^2 at each site, respectively. In contrast, the ClubMed site exhibited twice as much total biomass than the Mareto site (6.80 g vs. 3.26 g, respectively; Fig. 4), but the difference was not significant between the two sites (Wilcoxon-Mann-Whitney, W = 11, p-value = 0.10).

Behavioural observations

The behaviour of each individual eagle ray was observed during all surveys (Fig. 5, Tab. II). Among the 521 observations, four behaviours were frequently observed for rays at the ClubMed site: "swimming", where an individual or group of individuals swam against the current, which occurred in 96% of the observations; "chafing", where a ray was observed chafing against the substrate or using a cleaning station to remove ectoparasites (Berthe *et al.,* 2016a), which occurred in 25% of the observations; "pre-mating", where males were observed grasping on the back of females, which occurred in 7% of the observations; and "jumping", where rays jumped out of the water into the air, which occurred in 5% of the observations. Two behaviours were frequently observed at the Mareto site: "foraging", where rays were observed searching the substrate for food, which occurred in 79% of the observations and "swimming", which occurred in 18% of the observations. Lastly, an "escape" behaviour was also observed in eagle rays at both sites, where a ray would be noted swimming at least 50 m away from the foraging or swimming site when disturbed by a boat passing by, and this was observed in 17% of the eagle rays at the ClubMed site but in only 3% of the eagle rays at the Mareto site.

DISCUSSION

Our study revealed the distribution patterns of eagle rays between two sites in the lagoon of Moorea Island over one year (Fig. 3). Adult rays preferred ClubMed while juveniles were more abundant at Mareto. Our findings support life history strategies found in several shark species with an ontogenetic partitioning of the habitats (Grubbs, 2010). The ontogenetic stages induce different needs (*e.g.* specific diet or habitat), behaviours (*e.g.* solitaire or gregarious) or environmental adaptations (*e.g.* to low salinity, extreme temperature change, habitat shift) (*e.g.* Grubbs, 2010; Drymon *et al.,* 2014). In our study, we hypothesize that the energetic benefits of ontogenetic partitioning influence the distribution patterns of eagle rays at Moorea. Indeed, there were significant effects of three factors on spatial distribution of eagle rays at each site: current, wave direction, and prey availability (Fig. 3). The energetic costs for some activities, like swimming or foraging, can be a key to explaining distribution patterns. Due to the low tidal variation around Moorea (30 cm), the currents are largely induced by waves. Conrath and Musick (2010) speculated that swimming against a strong current is energetically costly for young eagle rays. In our study, juvenile rays forage at the Mareto site, which would be counterproductive if all of the energy gained from foraging was consumed swimming against a strong current, thus potentially explaining their low abundance at the site when there are strong currents. Thus, in addition to currents and waves affecting habitat choices, prey availability drives the habitat selection for many species (Schlaff *et al.*, 2014). Our two study sites offered the same level of diversity in terms of prey items, but showed different patterns of prey abundance (Fig. 4). Nevertheless, we need to take this result with caution as only one benthic survey was conducted. The Mareto site provided a high abundance of small prey items that would suit juvenile eagle rays. The ClubMed site had bigger but fewer prey items, and indeed, foraging activities were not frequently observed at ClubMed. Overall, ontogenetic partitioning induced by energetic needs may be an important adaptation that limits competition between life stages (Ajemian and Powers, 2015), and we assumed that it was the main driver dictating how eagle rays use the lagoon around Moorea Island. However, other environmental factors like water temperature or sex are also important in elasmobranch distribution patterns (Schlaff *et al.*, 2014), and also the anthropogenic noise could have a great impact on spatial distribution of many marine animals (Bertucci *et al.,* 2016; Nedelec *et al.,* 2016). Although we did not test the effects of boat noise on eagle rays distribution, we recorded an "escape" behaviour in eagle rays when a boat passed (17% of the eagle rays at the ClubMed site vs. 3% of the eagle rays at the Mareto site). Moreover, in a previous study on the north Coast of Moorea, Berthe and Lecchini (2016) showed that eagle rays stopped eating in the presence of boat noise. Anthropogenic noise is a form of pollution that increasingly contributes to natural soundscapes on a global scale and causes physiological, neurological, and hormonal problems (Francis and Barber, 2013; Simpson *et al.*, 2016).

The movement of one individual from Mareto to ClubMed during different ontogenetic stages represents evidence of ontogenetic shifts in habitat use from juveniles to adults. This movement could suggest that the two populations studied during this survey may in fact be one ontogenetically partitioned population. Our survey period spanned one year, and as elasmobranches are known to have a late maturity this could explain why only one individual, which had matured within the survey period, was observed in both sites. However, there are other habitats within the two sites, which could suit ocellated eagle rays: two passes (Opunohu Bay and Taotoi), a long channel in the lagoon and 8 km^2 of coral reefs. Our survey suggests that the Mareto site represents one stock of young eagle rays that can integrate different adult populations at least on the north coast of Moorea, if not further. To investigate this hypothesis, longer surveys must be done taking into account the age at maturity of *A. ocellatus* (Schluessel *et al.*, 2010). The photo-ID is one of the best ways to follow movement of the species because the pattern of the eagle rays fit the method and the species is easy to approach. The use of tracking tags would be a complementary way to follow the movement patterns of eagle rays in the lagoon of Moorea, especially on the north coast where tourism activities (thus jet-sky and boat traffic) are plentiful, and in the passes where the current is regularly strong and the visibility poor.

Overall, coral reef ecosystems are complex environments where all species are linked together and highly connected to human populations that are living near coastal areas. Understanding the drivers of habitat use by marine species is important to implement effective conservation strategies in the context of the increasing anthropogenic impact that islands like Moorea – an attractive island for local residents and for tourism – will continue to face. Our study examined the spatiotemporal distribution of eagle rays, according to ontogenetic stage, swimming behaviour and boat noise. Our findings could help increase the efficiency of conservation plans. Indeed, findings from this study provide information about the most suitable habitats for rays, and especially for juveniles, that are not currently protected by the management plan of Moorea Island, but need to be prioritized in any further revision (Oh *et al*., 2016). Prohibiting construction, limiting boat speed or boat traffic, regulating tourism activities – especially in those areas – are some recommendations that could improve the management of key species in coral reef ecosystems.

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